

tion of genetic diversity in tea (*Camellia sinensis*) using RAPD markers. *Genome* 38:201–210.
 Weir, B.S. 1996. Genetic data analysis. 2nd ed. Sinauer Assoc., Sunderland, England.
 Williams, J.G.K., A.R. Kubelik, K.J. Livak, J.A. Rafalski, and S.V.

Tingey. 1990. DNA polymorphism amplified by arbitrary primers are useful as genetic markers. *Nucl. Acids Res.* 18:6531–6535.
 Wright, S. 1969. Evolution and the genetics of populations, Vol. 2. The theory of gene frequencies. University of Chicago Press, Chicago, IL.

Blend Response and Stability and Cultivar Blending Ability in Oat

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ABSTRACT

Genetic diversity in cropping systems can provide buffering against varying environmental conditions. Therefore, cultivar blends may have greater and more stable yields than their pure-line components. Optimization of cultivar blend development requires knowledge of the relative importance of pure-line yield potential, blend response, and cultivar interactions to blend yield. Grain yield and volume weight of oat (*Avena sativa* L.) pure-line cultivars and cultivar blends were measured in eight Iowa environments in order to compare their productivity and stability and to estimate genetic components of blend yields. In one experiment, five early-maturing cultivars were grown as pure lines and as all possible two- and three-way cultivar blends. In a second experiment, ten midseason-maturing cultivars were grown as pure lines and as all possible two-way blends. Grain yield was 3% greater ($P < 0.05$) and volume weight was 1% greater ($P < 0.05$) in blends than in pure lines in the early-maturity experiment; however, pure line and blends did not differ in the midseason-maturity experiment. Blends had more stable ($P < 0.05$) yields than pure lines in the early-maturity experiment only. Modified diallel analysis was used to partition the variation among two-way blends into general yielding ability (GYA) and true general competitive ability (TGCA) of each component genotype, and specific competing ability (SCA) interaction between blend components. General yielding ability variation was significant, whereas variation for neither TGCA nor SCA was significant. Oat genotype responses to blending were sufficiently consistent across blending partners that superior blends can be selected based on pure-line evaluations of early-maturing cultivars.

OAT HECTARAGE IN THE USA has declined dramatically since 1950 (USDA-National Agricultural Statistics Service, 1998). Inclusion of oat in crop rotations, however, can enhance species diversity on farms and help to reduce weed and insect pests (Liebman and Dyck, 1993), increase soil quality and curb erosion (Gantzer et al., 1991), and stabilize farm incomes (Brummer, 1998). Because oat has value as feed for livestock, in human nutrition, and as a partial remedy for many production problems, methods to increase and stabilize oat grain yields are needed.

To minimize the adverse effects of environmental stresses on yield, plant breeders have attempted to develop cultivars that will perform reliably well across a range of years and sites (Evans, 1993; Allard and Bradshaw, 1964). Yield stability is the result of a crop's

buffering capacity, that is, its ability to adapt to variable weather, insect, disease, weed, and soil conditions. Ways to improve a crop's buffering capacity include intra-population interplant buffering through mixing cultivars or genotypes, and individual intraplant buffering through maintenance of heterozygosity (Allard and Bradshaw, 1964). A cultivar blend can capitalize on the principle of intra-population buffering, because a mixture of genetically different plants may have a greater chance of successful adaptation across a range of environments than a genetically homogeneous population.

Smithson and Lenné (1996) reviewed the literature on cultivar blends in many crops and concluded that blends generally yield slightly more than pure lines, but their true benefits lie in disease control and stability. Blending can have significant positive effects on disease control (Mundt et al., 1995; Finkh and Mundt, 1992; Power, 1991), and can reduce yield losses caused by variability in soil quality (Trimble and Fehr, 1983). The usefulness of cultivar blends in oat, however, has not been established definitively. Pfahler (1965) reported that a small sample of cultivar blends had greater yield stability than the component pure lines. Frey and Maldonado (1967) found that cultivar blends had significantly higher yields than their component pure-line cultivars only when in more stressful environments. Shorter and Frey (1979), by contrast, found no difference between blend and pure-line performance.

Comparisons of blends and pure lines can vary among samples of cultivars because of genotypic variation for contributions to blend performance. Gizlice et al. (1989) used a modified diallel analysis to characterize specific genotypic contributions to blend response. In this analysis, variation among blends was partitioned into general blending ability (GBA) and SCA variances. These effects are analogous to the general and specific combining abilities estimated from diallel analyses of single-cross hybrids in maize (*Zea mays* L.; Sprague and Tatum, 1942). Gizlice et al. (1989) demonstrated that if pure-line components are evaluated in the same experiment as the blends, then GBA can be partitioned into two components, GYA and TGCA. The GYA represents the innate yielding ability of a cultivar grown as a pure line, and the TGCA is the additional mean competitive response of a cultivar calculated as the difference be-

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tween the GBA and the GYA. If either TGCA or SCA effects are significant, blend yields would be expected to be significantly different than the average of their two component cultivars. Cultivars with positive TGCA effects are those that capitalize on or contribute to the stabilizing and buffering effects of blending.

Choosing the most efficient strategy for evaluating and selecting genotypes for use in blends requires knowledge of the relative importance of GYA, TGCA, and SCA effects in blends. If SCA effects are important, then superior blend combinations cannot be predicted on the basis of average blend responses of component cultivars or cultivar pure-line performance. In this case, as many combinations of genotypes as possible should be evaluated in order to have a good probability of identifying the best blends. If SCA effects are not important but variation for TGCA effects among cultivars exists, then superior blends can be developed by mixing genotypes with superior average blending responses. In this case, the most efficient breeding procedure would be to evaluate genotypes in blend combinations with a subset of tester genotypes and to select those genotypes with best average blending ability for use in blends. Finally, if blends are superior to pure lines but SCA effects are unimportant and variation among genotypes for TGCA effects is lacking, then superior blends can be identified simply on the basis of pure-line evaluations. Whereas Shorter and Frey (1979) performed a diallel analysis of oat blends and found that SCA effects were not important, they did not partition GBA into GYA and TGCA to identify optimal breeding procedures for blends. Furthermore, most of the genotypes in their study were selected from the same population, resulting in a limited sample of the genetic diversity available for use in oat cultivar blends. Estimation of the relative importance of GYA, TGCA, and SCA effects in a genetically broader sample of modern oat cultivars is needed to determine if blending current oat cultivars is warranted to enhance productivity or stability and to identify the most efficient method of identifying superior blends.

We investigated the effects of blending modern oat cultivars on grain yield and volume weight means and stabilities in two experiments. The objectives of these experiments were (i) to determine whether blend yields and volume weights were greater than those of pure lines, (ii) to compare yield stability of blends and pure lines, and (iii) to identify the genotypic sources of blend response in oat cultivar blends with the goal of providing breeders with a method for selecting effective cultivar combinations.

MATERIALS AND METHODS

Experimental Design and Observations

Two separate experiments were performed to evaluate early-maturing and midseason-maturing cultivars of oat. To simplify the mechanical harvesting of plots, blends were developed by mixing cultivars of the same maturity class. In the first trial, five early-maturing cultivars (Dane, Don, Horicon, Sheldon, and Starter) were grown as pure lines, all possible two-cultivar blends, and all possible three-cultivar blends for

a total of 25 entries. In the second trial, 10 midseason-maturing cultivars (Blaze, Burton, Chaps, Jerry, Jim, Newdak, Ogle, Prairie, Premier, and Rodeo) were evaluated as pure lines and as all two-way cultivar blends. With the addition of one experimental check line, IAR56-5, there were 56 entries in the midseason-maturity experiment. Blends were developed by compositing equal numbers of seeds of each component line and mixing thoroughly before planting.

Both experiments were grown during 1998 and 1999 at Ames (central Iowa), Nashua (northeastern Iowa), Crawfordsville (east central Iowa), and Lewis (west central Iowa). Soils at each location were: Nicollet silty loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll) at Ames, Readlyn loam (fine-loamy, mixed, mesic Aquic Hapludoll) at Nashua, Mahaska silty clay loam (fine, smectitic, mesic Aquic Argiudoll) at Crawfordsville, and Marshall silty clay loam (fine-silty, mixed, superactive, mesic Typic Hapludoll) at Lewis. The experimental designs were a 5×5 square lattice for the early-maturity experiment and a 7×8 rectangular lattice for the midseason experiment. There were three replications of each experiment within each environment. Plots were 3.72 m^2 and consisted of four rows, each spaced 30 cm apart. Plots were sown at a rate of 1000 seeds per plot.

Flowering date was recorded at Ames as the number of days after planting when 50% of the panicles in each plot were fully emerged. Reactions to natural infections of crown rust (*Puccinia coronata* Corda var. *avenae* W.P. Fraser and Ledingham) were rated twice at 1-wk intervals within the 2 wk following mean heading date of all entries at Ames and Nashua in both years. Ratings were based on a nine-point combined scale of incidence and severity (Holland et al., 1998). Plots were machine-harvested and grain yield (kg ha^{-1}) and volume weight (kg m^{-3}) were measured on every plot.

Statistical Analysis

Analyses of variance for each trait within and across environments were obtained using the SAS procedure general linear models (GLM; SAS Institute, 1985). Crossover genotype-by-environment interactions were identified as instances in which the difference between two genotypes' mean values was significantly ($P < 0.05$) positive in at least one environment and significantly negative in at least one other environment. A genotype's stability for yield and volume weight was estimated using Shukla's (1972) measure of genotype-by-environment interaction variance (σ_i^2),

$$\sigma_i^2 = \frac{p}{(p-2)(q-1)} \sum_{j=1}^q (X_{ij} - \bar{X}_i - \bar{X}_j + \bar{X}_{..})^2 - \frac{\text{SS(GE)}}{(p-1)(p-1)(q-1)}, \quad [1]$$

where

$$\text{SS(GE)} = \sum_{j=1}^q \sum_{i=1}^p (X_{ij} - \bar{X}_i - \bar{X}_j + \bar{X}_{..})^2, \quad [2]$$

and p is the number of genotypes, q is the number of environments, X_{ij} is the observed mean value of genotype i in environment j , and $\bar{X}_{..}$ is the overall mean. Grain yield and volume weight adaptabilities over environments were measured using Lin and Binns' (1988) superiority statistic, P_i , which is defined as

$$P_i = \frac{\sum_{j=1}^n (X_{ij} - M_j)^2}{(2n)}, \quad [3]$$

where X_{ij} is the mean value of the i th cultivar grown in the j th environment, M_j is the maximum mean response in the j th environment, and n is the number of environments tested. Sampling variances for P_i and σ_i^2 estimators were obtained with the jackknife procedure (Weir, 1996). Average stability and superiority of blends and pure lines were compared using a one-way analysis of variance in SAS procedure GLM (SAS Institute, 1985), in which the variation among entries within each group was used to test the significance of the mean differences.

Diallel analyses of yield and volume weight in both experiments were performed for blend response and blend performance per se according to Gizlice et al. (1989). Models from Federer et al. (1982) were used to describe our results for blends:

$$Y_{hij} = \mu + \rho_h + (\tau_i + \tau_j + \delta_i + \delta_j)/2 + \gamma_{ij} + \varepsilon_{hij} \quad [4]$$

and for pure lines:

$$Y_{hi} = \mu + \rho_h + \tau_i + \varepsilon_{hi} \quad [5]$$

In this model, Y_{hij} is a mean value for a blend of genotypes i and j over replications at one environment, μ is the general mean effect, ρ_h is the h th environmental effect, τ_i is the deviation of the i th pure-line genotype from the mean of all pure lines (two times GYA), $\delta_i/2$ is the TGCA of the i th genotype (in blends), γ_{ij} is the SCA of genotypes i and j when grown together, and ε_{hij} is a genotype-by-environment interaction effect. TGCA effects were estimated from the analysis of blend response. The genotype-by-environment effect was further partitioned into GYA-by-environment, TGCA-by-environment, and SCA-by-environment effects. Mean squares for each effect were calculated using the SAS procedure GLM (SAS Institute, 1985). Mean separations were based on Fisher's protected LSD at $P < 0.05$.

RESULTS AND DISCUSSION

Effects of Blending on Grain Yield and Volume Weight

Average grain yields and volume weights varied among the eight environments (Table 1). Highest yields were observed at Ames in 1999, with average yields of 4248 kg ha⁻¹ for the early-maturity experiment and 4787 kg ha⁻¹ for the midseason-maturity experiments. The environment with the lowest yields was Crawfordsville in 1998, where the average yields were only 1867 kg ha⁻¹ in the early-maturity experiment and 1762 kg ha⁻¹ in the midseason-maturity experiment. Mean volume weights ranged from 433 to 464 kg m⁻³ and 450 to 551 kg m⁻³ across environments in the early and midseason-maturity experiments, respectively. Crown rust infection was observed in all environments, but disease reaction scores did not differ among pure-line cultivars in any environment in which they were measured. Thus, it is unlikely that crown rust resistance contributed to blend responses in this study.

Mean blend response averaged over environments was positive in the early-maturity but not the midseason-maturity experiment (Tables 1–5). It is not obvious why blend responses were observed in the early-maturity but not the midseason-maturity cultivars. This result may be due to sampling different genotypes in the different experiments, or may indicate that intra-genotypic com-

Table 1. Overall mean, blend response, and percentage blend response for yield and volume weight within each of eight Iowa environments for 5 early-maturity oat cultivars and their 10 two-way and 10 three-way blends, and for 10 midseason-maturity oat cultivars and their 45 two-way blends.

| Environment | Early-maturity cultivars | | | | | | Mid-season maturity cultivars | | | | | |
|----------------------|--------------------------|----------------|------------------|---------------|----------------|------------------|-------------------------------|----------------|------------------|---------------|----------------|------------------|
| | Yield | | | Volume weight | | | Yield | | | Volume weight | | |
| | Mean | Blend response | % Blend response | Mean | Blend response | % Blend response | Mean | Blend response | % Blend response | Mean | Blend response | % Blend response |
| Ames, 1998 | 3808 | 168** | 4.6 | 433 | 11** | 2.5 | 4065 | 50 | 1.2 | 450 | -2 | -0.4 |
| Crawfordsville, 1998 | 1867 | 122 | 6.9 | 436 | 6 | 1.4 | 1762 | -42 | -2.4 | 466 | 8** | 1.7 |
| Lewis, 1998 | 2592 | 159 | 6.5 | 464 | -1 | -0.2 | 3349 | 9 | 0.3 | 479 | 4 | 0.8 |
| Nashua, 1998 | 3175 | 202** | 6.7 | 460 | 9 | 2.0 | 3305 | 50 | 1.5 | 495 | -1 | -0.2 |
| 1998 Average | 2859 | 163** | 6.0 | 448 | 6* | 1.4 | 3120 | 17 | 0.5 | 473 | 2 | 0.4 |
| Ames, 1999 | 4248 | 74 | 1.8 | 493 | -12** | -2.5 | 4787 | 2 | 0.0 | 501 | 2 | 0.4 |
| Crawfordsville, 1999 | 4200 | -25 | -0.6 | 493 | 8** | 1.6 | 4437 | 171* | 4.0 | 497 | -5* | -1.0 |
| Lewis, 1999 | 3360 | 17 | 0.5 | 478 | 5 | 1.1 | 3683 | 46 | 1.3 | 469 | -6 | -1.3 |
| Nashua, 1999 | 3313 | 55 | 1.7 | 542 | 13*** | 2.4 | 3469 | -111* | -3.1 | 551 | -1 | -0.2 |
| 1999 Average | 3780 | 30 | 0.8 | 502 | 4 | 0.8 | 4094 | 27 | 0.7 | 505 | -2 | -0.4 |
| Overall Mean | 3320 | 102* | 3.1 | 475 | 5* | 1.1 | 3607 | 22 | 0.6 | 489 | 0 | 0.0 |

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

Table 2. Mean heading date, grain yield, volume weight, Shukla's genotype-by-environment stability variance (σ_i^2), and Lin and Binn's (1988) adaptability parameter (P_i) for five early-maturing pure-line oat cultivars and 10 two-way and 10 three-way cultivar blends evaluated at eight Iowa environments.

| Cultivar or blend | Heading date | Grain yield | % Blend response | Grain yield stability | | Volume weight | % Blend response | Volume weight stability | |
|-----------------------------|------------------|---------------------|------------------|----------------------------|-----------------------------------|--------------------|------------------|----------------------------|--------------|
| | | | | $P_i \times 10^{\ddagger}$ | $\sigma_i^2 \times 10^{\ddagger}$ | | | $P_i \times 10^{\ddagger}$ | σ_i^2 |
| | DAP [†] | kg ha ⁻¹ | | | | kg m ⁻³ | | | |
| Dane | 70 | 3558 | | 34 | 73 | 449 | | 329 | 313 |
| Don | 71 | 3107 | | 57 | 33 | 479 | | 81 | 197 |
| Horicon | 76 | 3413 | | 29 | 153 | 473 | | 94 | 135 |
| Sheldon | 74 | 3091 | | 85 | 69 | 458 | | 209 | 102 |
| Starter | 72 | 3013 | | 83 | 29 | 495 | | 16 | 153 |
| Dane/Don | 70 | 3477 | 4.3 | 17 | 22 | 467 | 0.6 | 148 | 88 |
| Dane/Horicon | 71 | 3488 | 0.1 | 13 | 12 | 465 | 1.3 | 150 | 70 |
| Dane/Sheldon | 70 | 3558 | 7.0 | 19 | 43 | 464 | 3.2 | 162 | 46 |
| Dane/Starter | 71 | 3400 | 3.5 | 20 | 66 | 477 | 0.6 | 72 | 14 |
| Don/Horicon | 70 | 3217 | -1.3 | 62 | 63 | 477 | -2.3 | 84 | 113 |
| Don/Sheldon | 72 | 3245 | 4.7 | 41 | 34 | 476 | 1.4 | 80 | 68 |
| Don/Starter | 71 | 3110 | 1.6 | 60 | 54 | 486 | -1.9 | 66 | 389 |
| Horicon/Sheldon | 71 | 3296 | 1.3 | 38 | 63 | 474 | -0.3 | 96 | 57 |
| Horicon/Starter | 71 | 3263 | 1.5 | 34 | 19 | 491 | -0.4 | 19 | 32 |
| Sheldon/Starter | 71 | 3155 | 3.4 | 55 | 57 | 488 | 0.1 | 38 | 285 |
| Dane/Don/Horicon | 73 | 3489 | 3.9 | 16 | 25 | 467 | 2.1 | 133 | 22 |
| Dane/Don/Sheldon | 73 | 3477 | 2.2 | 18 | 42 | 468 | 5.1 | 137 | 57 |
| Dane/Don/Starter | 71 | 3251 | 0.8 | 36 | 43 | 475 | 1.2 | 96 | 92 |
| Dane/Horicon/Sheldon | 72 | 3521 | 5.0 | 14 | 61 | 475 | 3.5 | 91 | 102 |
| Dane/Horicon/Starter | 72 | 3507 | 5.4 | 12 | 13 | 478 | 0.3 | 79 | 61 |
| Dane/Sheldon/Starter | 71 | 3368 | 4.6 | 29 | 29 | 482 | 4.0 | 54 | 70 |
| Don/Horicon/Sheldon | 73 | 3279 | 2.3 | 44 | 73 | 475 | 0.8 | 85 | 108 |
| Don/Horicon/Starter | 73 | 3208 | 1.0 | 45 | 15 | 480 | -0.3 | 77 | 212 |
| Don/Sheldon/Starter | 72 | 3224 | 5.0 | 40 | 44 | 473 | 2.9 | 116 | 242 |
| Horicon/Sheldon/Starter | 73 | 3243 | 2.2 | 42 | 16 | 481 | 2.7 | 62 | 106 |
| LSD (0.05) | 2 | 212 | | 15 | 40 | 11 | | 38 | 79 |
| Mean of all pure-lines | 73 | 3236 | | 58 | 71 | 471 | | 146 | 180 |
| Mean of all blends | 72 | 3339 | 3.2 | 33 | 40 | 476 | 1.1 | 92 | 112 |
| Mean 2-way blend response | | 84* | 2.6 | -22* | -28 | 5* | 1.1 | -54 | -64 |
| Mean 3-way blend response | | 120* | 3.7 | -28* | -35 | 4* | 0.8 | -53 | -73 |
| Mean overall blend response | | 102* | 3.2 | -25* | -32* | 5* | 1.1 | -54 | -68 |

* Significant at the 0.05 probability level.

† Days after planting.

‡ Actual values equal to reported value times the indicated factor.

petition for resources is stronger than inter-genotypic competition when plants mature more quickly.

Within environments, mean blend yields were less than mean pure-line yields at Nashua in 1999 in the mid-season-maturity experiment. Mean blend yields were greater than mean pure-line yields at Ames and Nashua in 1998 for the early-maturity experiment, and at Crawfordville in 1999 for the midseason-maturity experiment. Mean percentage blend response and environment mean yield (Table 1) were negatively correlated in the early-maturity experiment ($r = -0.72$, $P < 0.05$), congruent with Frey and Maldonado's (1967) finding that oat blending response increased in more stressful environments. In the early-maturity experiment, the greatest-yielding pure line, Dane, had grain yield equal to the greatest-yielding blend, Dane/Sheldon (Table 2). The highest-ranking entry in the midseason-maturity experiment was a blend (Chaps/Jim), but it was not different than the best pure line (Chaps) (Table 3). These results suggest that oat cultivar blends may provide buffering against stressful environments and provide a low-risk opportunity for slightly greater grain yields, if appropriate cultivar mixtures are chosen.

Averaged over environments, blend volume weights were greater than pure-line volume weights in the early-maturity experiment, but not in the midseason-maturity

experiment (Tables 1–5). The entry with the highest ranking for volume weight in the early-maturity experiment was a pure line, Starter (Table 2), but Starter was not different than the highest ranked blend, Horicon/Starter. In the midseason-maturity experiment, the pure line with the highest volume weight, Jerry, was not different from the best blends, Blaze/Jerry and Jerry/Premier (Table 3). In both experiments, the blend with the highest volume weight included the best pure line, suggesting that blend performance was largely determined by pure-line performance. Because the highest-ranked entries for volume weight in both experiments were pure-line cultivars, and because grain uniformity may be important to farmers who market their grain for milling for human consumption, blending may have unfavorable effects on volume weight. Farmers wishing to use blends should grow cultivar blends that will produce sufficient grain uniformity to satisfy their marketing needs.

Two- and three-component blend yields and volume weights were compared in the early-maturity experiment. No difference existed between the two types of blends for either grain yield or volume weight (Tables 2 and 4). The mean yields of two- and three-way blends were 3321 and 3356 kg ha⁻¹, respectively, and the mean volume weights of two- and three-way blends were 476

Table 3. Heading date, grain yield, volume weight, Shukla's genotype-by-environment stability variance (σ_i^2), and Lin and Binn's adaptability parameter (P_i) for 10 midseason-maturing pure-line oat cultivars and 45 two-way cultivar blends evaluated at eight Iowa environments.

| Cultivar or blend | Heading date | Grain yield | % Blend response | Grain yield stability | | Volume weight | % Blend response | Volume weight stability | |
|------------------------|------------------|---------------------|------------------|-----------------------------|------------------------------------|--------------------|------------------|----------------------------|--------------|
| | | | | $P_i \times 10^{4\ddagger}$ | $\sigma_i^2 \times 10^{3\ddagger}$ | | | $P_i \times 10^{\ddagger}$ | σ_i^2 |
| | DAP [†] | kg ha ⁻¹ | | | | kg m ⁻³ | | | |
| Blaze | 74 | 3868 | | 19 | 81 | 508 | | 84 | 282 |
| Burton | 76 | 3262 | | 98 | 62 | 485 | | 266 | 198 |
| Chaps | 74 | 3950 | | 13 | 30 | 482 | | 276 | 124 |
| Jerry | 74 | 3278 | | 111 | 67 | 531 | | 2 | 37 |
| Jim | 74 | 3885 | | 21 | 49 | 496 | | 169 | 209 |
| Newdak | 75 | 3077 | | 157 | 142 | 470 | | 409 | 342 |
| Ogle | 75 | 3546 | | 60 | 100 | 465 | | 498 | 154 |
| Prairie | 75 | 3645 | | 36 | 78 | 455 | | 657 | 418 |
| Premier | 75 | 3455 | | 60 | 39 | 509 | | 72 | 177 |
| Rodeo | 78 | 3932 | | 13 | 104 | 477 | | 340 | 269 |
| Blaze/Burton | 75 | 3423 | -4.0 | 84 | 113 | 494 | -0.5 | 191 | 592 |
| Blaze/Chaps | 75 | 3926 | 0.4 | 15 | 33 | 496 | 0.2 | 152 | 141 |
| Blaze/Jerry | 74 | 3711 | 3.9 | 43 | 196 | 520 | 0.1 | 42 | 457 |
| Blaze/Jim | 73 | 3950 | 1.9 | 14 | 39 | 500 | -0.3 | 122 | 151 |
| Blaze/Newdak | 75 | 3522 | 1.4 | 70 | 116 | 486 | -0.6 | 232 | 161 |
| Blaze/Ogle | 76 | 3815 | 2.9 | 22 | 36 | 487 | 0.1 | 223 | 72 |
| Blaze/Prairie | 75 | 3703 | -1.4 | 38 | 59 | 483 | 0.2 | 282 | 276 |
| Blaze/Premier | 74 | 3707 | 1.2 | 31 | 68 | 511 | 0.5 | 59 | 139 |
| Blaze/Rodeo | 76 | 4033 | 3.4 | 6 | 23 | 495 | 0.4 | 171 | 352 |
| Burton/Chaps | 74 | 3562 | -1.2 | 54 | 60 | 482 | -0.3 | 285 | 156 |
| Burton/Jerry | 73 | 3345 | 2.3 | 89 | 57 | 507 | -0.2 | 78 | 126 |
| Burton/Jim | 73 | 3465 | -3.1 | 66 | 40 | 489 | -0.1 | 223 | 222 |
| Burton/Newdak | 76 | 3256 | 2.7 | 104 | 56 | 483 | 1.1 | 278 | 304 |
| Burton/Ogle | 77 | 3419 | 0.4 | 76 | 34 | 475 | 0.0 | 385 | 268 |
| Burton/Prairie | 77 | 3299 | -4.5 | 88 | 50 | 469 | -0.1 | 475 | 585 |
| Burton/Premier | 75 | 3196 | -4.9 | 110 | 25 | 495 | -0.3 | 171 | 192 |
| Burton/Rodeo | 77 | 3509 | -2.4 | 58 | 31 | 483 | 0.4 | 308 | 646 |
| Chaps/Jerry | 74 | 3676 | 1.7 | 36 | 23 | 511 | 0.9 | 60 | 62 |
| Chaps/Jim | 75 | 4101 | 4.7 | 11 | 122 | 496 | 1.5 | 153 | 105 |
| Chaps/Newdak | 73 | 3591 | 2.2 | 53 | 38 | 482 | 1.1 | 276 | 87 |
| Chaps/Ogle | 75 | 3815 | 1.8 | 28 | 88 | 478 | 1.0 | 340 | 237 |
| Chaps/Prairie | 76 | 3686 | -2.9 | 33 | 47 | 465 | -0.8 | 507 | 266 |
| Chaps/Premier | 76 | 3745 | 1.1 | 27 | 29 | 499 | 0.7 | 127 | 94 |
| Chaps/Rodeo | 76 | 3898 | -1.1 | 15 | 58 | 473 | -1.4 | 390 | 124 |
| Jerry/Jim | 75 | 3664 | 2.3 | 44 | 53 | 516 | 0.5 | 50 | 344 |
| Jerry/Newdak | 75 | 3255 | 2.4 | 115 | 85 | 506 | 1.0 | 92 | 264 |
| Jerry/Ogle | 75 | 3564 | 4.4 | 58 | 50 | 493 | -0.9 | 183 | 297 |
| Jerry/Prairie | 75 | 3424 | -1.1 | 76 | 32 | 493 | -0.1 | 177 | 18 |
| Jerry/Premier | 75 | 3420 | 1.6 | 77 | 61 | 520 | 0.0 | 42 | 377 |
| Jerry/Rodeo | 76 | 3558 | -1.3 | 62 | 69 | 500 | -0.7 | 129 | 185 |
| Jim/Newdak | 74 | 3649 | 4.8 | 54 | 177 | 484 | 0.3 | 251 | 112 |
| Jim/Ogle | 75 | 3775 | 1.6 | 29 | 52 | 484 | 0.8 | 296 | 416 |
| Jim/Prairie | 74 | 3824 | 1.6 | 24 | 132 | 478 | 0.6 | 362 | 474 |
| Jim/Premier | 74 | 3678 | 0.2 | 33 | 41 | 504 | 0.2 | 122 | 305 |
| Jim/Rodeo | 73 | 3971 | 1.6 | 12 | 30 | 488 | 0.3 | 226 | 130 |
| Newdak/Ogle | 74 | 3394 | 2.5 | 85 | 62 | 469 | 0.3 | 418 | 38 |
| Newdak/Prairie | 75 | 3411 | 1.5 | 73 | 69 | 463 | -0.1 | 516 | 111 |
| Newdak/Premier | 75 | 3221 | -1.4 | 126 | 80 | 489 | -0.2 | 217 | 171 |
| Newdak/Rodeo | 76 | 3561 | 1.6 | 54 | 22 | 474 | -0.1 | 370 | 143 |
| Ogle/Prairie | 76 | 3658 | 1.7 | 37 | 150 | 455 | -1.1 | 674 | 513 |
| Ogle/Premier | 76 | 3591 | 2.6 | 47 | 83 | 481 | -1.4 | 326 | 352 |
| Ogle/Rodeo | 77 | 3746 | 0.2 | 35 | 59 | 463 | -1.8 | 519 | 81 |
| Prairie/Premier | 76 | 3432 | -3.3 | 67 | 67 | 475 | -1.6 | 380 | 265 |
| Prairie/Rodeo | 77 | 3691 | -2.6 | 37 | 76 | 470 | 0.7 | 492 | 1034 |
| Premier/Rodeo | 74 | 3691 | -0.1 | 31 | 42 | 484 | -1.9 | 259 | 93 |
| LSD (0.05) | 3 | 233 | | 17 | 40 | 14 | | 71 | 181 |
| Mean of all pure-lines | 75 | 3590 | | 59 | 75 | 488 | | 277 | 221 |
| Mean of all blends | 75 | 3612 | 0.6 | 52 | 65 | 488 | 0.0 | 256 | 209 |
| Mean blend response | | 22 | 0.6 | -7 | -10 | 0 | 0.0 | -21 | 31 |

[†] Days after planting.[‡] Actual values equal to reported value times indicated factor.

and 475 kg m⁻³, respectively. Increasing the number of cultivars included in a blend increases genetic diversity, but it did not affect blend performance. Frey and Maldonado (1967) obtained similar results from comparisons of two to six component blends in oat, and Clay and Allard (1969) concluded that barley (*Hordeum vulgare*

L.) blends containing up to 10 components were no better than two-way blends.

Effects of Blending on Stability

Three of the ten possible comparisons of pure-line cultivars in the early-maturity experiment exhibited signifi-

Table 4. Analysis of variance of blend response and blend yield per se for grain yield and volume weight of five early-maturing oat cultivars and all possible two- and three-way cultivar blends grown at eight Iowa environments.

| Source of variation | df | Yield | | df | Volume weight | |
|-----------------------------------|-----|----------------------------------|--|-----|----------------------|------------------|
| | | $MS_{\text{per se}} \times 10^3$ | $MS_{\text{BR}} \parallel \times 10^3$ | | $MS_{\text{per se}}$ | MS_{BR} |
| Environments | 7 | 16 223‡ | | 7 | 31 304‡ | |
| Entries | 24 | 210‡ | | 24 | 784‡ | |
| Pure lines (GYA)# | 4 | 445** | | 4 | 2 416‡ | |
| Blends | 19 | 154‡ | | 19 | 452‡ | |
| 2-way Blends | 9 | 184† | | 9 | 742‡ | |
| GBA and TGCA††‡‡ | 4 | 395† | 96 | 4 | 1 576† | 136 |
| SCA§§ | 5 | 16 | 16 | 5 | 25 | 25 |
| 3-way Blends | 9 | 135† | | 9 | 207 | |
| Blends vs. Pure lines | 1 | 335** | | 1 | 563* | |
| 2-way Blends vs. Pure lines | 1 | 190* | | 1 | 934* | |
| 3-way Blends vs. Pure lines | 1 | 385** | | 1 | 533* | |
| 2-way vs. 3-way Blends | 1 | 51 | | 1 | 50 | |
| Entry × Environment | 168 | 46† | | 168 | 136† | |
| Pure line × Environment | 28 | 78† | | 28 | 196* | |
| Blends × Environment | 133 | 40† | | 133 | 113† | |
| 2-way Blend × Environment | 63 | 44** | | 63 | 120† | |
| GBA/TGCA × Environment§ | 28 | 55† | 52** | 28 | 166† | 167† |
| SCA × Environment§ | 35 | 35 | 35 | 35 | 76* | 76* |
| 3-way Blend × Environment | 63 | 38* | | 63 | 107† | |
| Blend vs. Pure line × Environment | 7 | 91† | | 7 | 339† | |
| Error | | 285 | 26 | | 285 | 52 |

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† Significant at the 0.005 probability level.

‡ Significant at the 0.0001 probability level.

§ $MS_{\text{per se}}$ = mean squares for the variable per se correspond to variance due to GBA. Mean squares for blend residuals adjusted for GYA effects correspond to variance due to TGCA.¶ MS_{BR} = mean squares based on blend response entry residuals obtained by subtracting the mean of component pure lines.

GYA = general yielding ability.

†† GBA = general blending ability.

‡‡ TGCA = true general competing ability.

§§ SCA = specific competing ability.

cant crossover genotype-by-environment interactions for grain yield. In the midseason-maturity experiment, among 45 pure-line cultivar comparisons, 10 comparisons of yield and 6 of volume weight exhibited significant crossover genotype-by-environment interactions. The existence of numerous significant genotype-by-environment interactions among a set of elite cultivars

within the target set of Iowa oat-growing environments suggests that improvements in yield stability, as well as yield potential, are desirable. We used two statistics to measure the stability or adaptability of the entries in our experiment to determine if blending cultivars results in improved stability of grain yield or volume weight.

Shukla's stability variance (Shukla, 1972) is an unbi-

Table 5. Analysis of variance of blend response and blend yield per se for grain yield and volume weight of 10 midseason-maturing oat cultivars and all possible two-cultivar blends grown at eight Iowa environments.

| Source of variation | df | Yield | | df | Volume weight | |
|-----------------------------------|-----|----------------------------------|--|-----|----------------------|------------------|
| | | $MS_{\text{per se}} \times 10^3$ | $MS_{\text{BR}} \parallel \times 10^3$ | | $MS_{\text{per se}}$ | MS_{BR} |
| Environments | 7 | 49 595‡ | | 7 | 53 331‡ | |
| Entries | 54 | 514‡ | | 54 | 2 302‡ | |
| Pure lines (GYA)# | 9 | 923‡ | | 9 | 4 282‡ | |
| Blends | 44 | 440‡ | | 44 | 1 949‡ | |
| GBA and TGCA††‡‡ | 9 | 1 800† | 199 | 9 | 9 091† | 192 |
| SCA§§ | 35 | 30 | 30 | 35 | 102 | 102 |
| Blends vs. Pure lines | 1 | 90 | | 1 | 1 | |
| Entry × Environment | 378 | 52† | | 378 | 210† | |
| Pure line × Environment | 63 | 55† | | 63 | 187† | |
| Blends × Environment | 308 | 51† | | 308 | 216† | |
| GCB/TGCA × Environment§ | 63 | 129† | 221*** | 63 | 674† | 368† |
| SCA × Environment§ | 245 | 36* | 36* | 245 | 98 | 98 |
| Blend vs. Pure line × Environment | 7 | 78† | | 7 | 181† | |
| Error | 440 | 30 | | 440 | 66 | |

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† Significant at the 0.005 probability level.

‡ Significant at the 0.0001 probability level.

§ $MS_{\text{per se}}$ = mean squares for the variable per se correspond to variance due to GBA. Mean squares for blend residuals adjusted for GYA effects correspond to variance due to TGCA.¶ MS_{BR} = mean squares based on blend response entry residuals obtained by subtracting the mean of component pure lines.

GYA = general yielding ability.

†† GBA = general blending ability.

‡‡ TGCA = true general competing ability.

§§ SCA = specific competing ability.

ased estimate of the genotype-by-environment interaction variance for a given genotype. According to Shukla (1972), cultivars with smaller genotype-by-environment interaction variances (σ_i^2) are more stable. On average, Shukla's genotype-by-environment stability variance was smaller for blends than pure lines in the early-maturity experiment, but not the midseason-maturity experiment (Tables 2 and 3). Although volume weight stability was not significantly better in blends than in pure lines, the blend with the smallest Shukla's variance for volume weight in the early-maturity experiment (Dane/Starter) was significantly more stable than the most stable pure line (Sheldon) (Table 2).

One disadvantage of Shukla's stability measure is that it does not provide any information on the magnitude of yield of the cultivars. A cultivar that has a constant response to environments may be very stable, but if it is consistently lower yielding, it is not useful to the producer. Lin and Binns' (1988) adaptability parameter (P_i) compares the yields of test cultivars with the greatest-yielding cultivar within each location in the experiment, rather than with the mean yield of all cultivars. Smaller values of P_i reflect greater adaptability of an entry across environments. The difference between Shukla's stability variance and Lin and Binns' adaptability parameter is demonstrated by their correlations with mean yield in this study. In the midseason-maturity experiment, Shukla's variance had no correlation with mean yield ($r = -0.039$, $P = 0.78$), demonstrating that a cultivar's yield potential has little to do with its stability. Lin and Binns' adaptability parameter, however, was highly negatively correlated with grain yield ($r = -0.964$, $P < 0.0001$) because the adaptability parameter measures the magnitude as well as the consistency of yield across environments. Blends were significantly better adapted than pure lines on average, according to Lin and Binns' adaptability parameter for yield in the early-maturity trial, but were not different than pure lines in the midseason experiment (Tables 2 and 3).

Competing Ability Analysis

Our results indicated that oat yields can sometimes be increased through the blending of particular cultivars. However, all blends were not better than all pure lines, and blend response was not consistent among all blends, so methods for identifying superior blends would be helpful to farmers and plant breeders. Comparison of the relative importance of variation in GYA, GBA, TGCA, and SCA effects can guide breeding efforts aimed at developing improved cultivar blends. SCA and TGCA are measures of blending performance that exclude innate pure-line yielding effects (GYA). In our experiments, SCA effects were not significant (Tables 4 and 5), indicating that statistical interactions between cultivars in blends were not important. This lack of SCA simplifies the identification of superior blends because it makes expensive evaluations of all possible blend combinations unnecessary.

Variation among TGCA effects was also not significant in both experiments (Tables 4–7). This implies that no

Table 6. General blending ability (GBA), general yielding ability (GYA), and true general competing ability (TGCA) effects for yield and volume weight of five early-maturing spring oat cultivars grown as pure lines and all possible two-way blends in eight Iowa environments. τ_i = the deviation of the i th pure-line genotype from the mean of all pure lines, and $\delta_i/2$ = the TGCA of the i th genotype.

| Cultivar | Yield | | | Volume weight | | |
|------------|------------------------------------|-----------------------|--------------------------|------------------------------------|-----------------------|--------------------------|
| | GBA ($\tau_i/2 + \delta_i/2$) | GYA ($\tau_i/2$) | TGCA ($\delta_i/2$) | GBA ($\tau_i/2 + \delta_i/2$) | GYA ($\tau_i/2$) | TGCA ($\delta_i/2$) |
| | kg ha ⁻¹ | | | kg m ⁻³ | | |
| Dane | 255 | 161 | 94 | -50 | -11 | 4 |
| Don | -36 | -65 | 28 | 3 | 4 | -1 |
| Horicon | 35 | 88 | -53 | 5 | 1 | 3 |
| Sheldon | 32 | -73 | 105 | -4 | -6 | 6 |
| Starter | 77 | -111 | 35 | 62 | 12 | 3 |
| Mean | 42 | 0 | 42 | 3 | 0 | 3 |
| LSD (0.05) | 98 | 106 | NS† | 5 | 5 | NS |

† NS = not significant at $P > 0.05$.

cultivar has a general blending ability that is significantly better or worse than others. The average of cultivar TGCA effects is equal to half the mean blend response. The significance of blend response in the early-maturity experiment indicates that the mean TGCA effect of early-maturity cultivars was greater than zero; nevertheless, there was no significant variation among cultivar TGCA effects. This implies that while early-maturity cultivars in general responded positively to blending, the positive blend response was sufficiently consistent among cultivars that superior blend components can be selected efficiently on the basis of pure-line evaluations. Testing of oat blends is not necessarily required to identify superior blend components. Further evidence of this was that the significant pure-line GYA and GBA effects for grain yield and volume weight in the early- and midseason-maturity experiments (Tables 6 and 7) were highly correlated ($r = 0.85$, $P < 0.01$ for effects on yield in the early-maturity experiment, and $r = 0.95$, $P < 0.0001$ for effects on yield in the midseason-maturity experiment). Finally, blends of the greatest-yielding pure lines within each experiment (Dane/Horicon in

Table 7. General blending ability (GBA), general yielding ability (GYA), and true general competing ability (TGCA) effects for yield and volume weight of 10 midseason-maturing spring oat cultivars grown as pure lines and all possible two-way blends in eight Iowa environments. τ_i = the deviation of the i th pure-line genotype from the mean of all pure lines, and $\delta_i/2$ = the TGCA of the i th genotype.

| Cultivar | Yield | | | Volume weight | | |
|------------|------------------------------------|-----------------------|--------------------------|------------------------------------|-----------------------|--------------------------|
| | GBA ($\tau_i/2 + \delta_i/2$) | GYA ($\tau_i/2$) | TGCA ($\delta_i/2$) | GBA ($\tau_i/2 + \delta_i/2$) | GYA ($\tau_i/2$) | TGCA ($\delta_i/2$) |
| | kg ha ⁻¹ | | | kg m ⁻³ | | |
| Blaze | 171 | 139 | 22 | 10 | 10 | 0 |
| Burton | -243 | -164 | -106 | -2 | -1 | 0 |
| Chaps | 198 | 180 | 14 | -1 | -3 | 2 |
| Jerry | -100 | -156 | 46 | 22 | 21 | 1 |
| Jim | 207 | 148 | 48 | 6 | 4 | 2 |
| Newdak | -195 | -256 | 34 | -7 | -9 | 2 |
| | 45 | -22 | 93 | -13 | -12 | -2 |
| Prairie | -36 | 28 | -51 | -17 | -16 | -1 |
| Premier | -92 | -68 | -8 | 9 | 11 | -2 |
| Rodeo | 155 | 171 | 18 | -7 | -5 | -2 |
| Mean | 11 | 0 | 11 | 0 | 0 | 0 |
| LSD (0.05) | 101 | 116 | NS† | 7 | 7 | NS |

† NS = not significant at $P > 0.05$.

the early-maturity experiment and Chaps/Rodeo in the midseason-maturity experiment) were not significantly different than the best blends within each experiment for yield (Tables 2 and 3).

The ability to successfully develop superior cultivar blends on the basis of pure-line performance is advantageous to both plant breeders and farmers. For plant breeders, the high correlation of pure-line performance and general blending ability and the lack of cultivar-cultivar interactions simplifies and reduces costs of blend breeding procedures. In addition, farmers can successfully select the component cultivars for blending simply by choosing those cultivars best adapted to their region based on cultivar evaluation trial data.

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REFERENCES

- Allard, R.W., and A.D. Bradshaw. 1964. Implications of genotype-environmental interactions in applied plant breeding. *Crop Sci.* 4:503–508.
- Brummer, E.C. 1998. Diversity, stability, and sustainable American agriculture. *Agron. J.* 90:1–2.
- Clay, R.E., and R.W. Allard. 1969. A comparison of the performance of homogeneous and heterogeneous barley populations. *Crop Sci.* 9:407–412.
- Evans, L.T. 1993. *Crop evolution, adaptation, and yield*. Cambridge University Press, Cambridge.
- Federer, W.T., J.C. Connigale, J.N. Rutger, and A. Wijesinha. 1982. Statistical analyses of yields from uniblennds and biblennds of eight dry bean cultivars. *Crop Sci.* 22:111–115.
- Finkh, M.R., and C.C. Mundt. 1992. Stripe rust, yield, and plant competition in wheat cultivar mixtures. *Phytopathology* 82:905–913.
- Frey, K.J., and U. Maldonado. 1967. Relative productivity of homogeneous and heterogeneous oat cultivars in optimum and suboptimum environments. *Crop Sci.* 7:532–535.
- Gantzer, C.J., S.H. Anderson, A.L. Thompson, and J.R. Brown. 1991. Evaluation of soil loss after one hundred years of soil and crop management. *Agron. J.* 83:74–77.
- Gizlice, Z., T.E. Carter, J.W. Burton, and T.E. Emigh. 1989. Partitioning of blending ability using two-way blends and component lines of soybean. *Crop Sci.* 29:885–889.
- Holland, J.B., D.V. Uhr, D. Jeffers, and M.M. Goodman. 1998. Inheritance of resistance to southern corn rust in tropical-by-corn-belt maize populations. *Theor. Appl. Genet.* 96:232–241.
- Liebman, M., and E. Dyck. 1993. Crop rotation and intercropping strategies for weed management. *Ecol. Applic.* 3:92–122.
- Lin, C.S., and M.R. Binns. 1988. A superiority measure of cultivar performance for cultivar \times location data. *Can. J. Plant Sci.* 68:193–198.
- Mundt, C.C., L.S. Brophy, and M.S. Schmitt. 1995. Choosing crop cultivars and cultivar mixtures under low versus high disease pressure: a case study with wheat. *Crop Prot.* 14:509–515.
- Pfahler, P.L. 1965. Environmental variability and genetic diversity within populations of oats (cultivated species of *Avena*) and rye (*Secale cereale* L.). *Crop Sci.* 5:271–275.
- Power, H.G. 1991. Virus spread and vector dynamics in genetically diverse populations. *Ecology* 82:232–241.
- SAS Institute. 1985. *SAS user's guide: Statistics*. 5th ed. SAS Inst., Cary, NC.
- Shorter, R., and K.J. Frey. 1979. Relative yields of mixtures and monocultures of oat genotypes. *Crop Sci.* 19:548–553.
- Shukla, G.K. 1972. Some statistical aspects of partitioning genotype-environmental components of variability. *Heredity* 29:237–245.
- Smithson, J.B., and J.M. Lenné. 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Ann. Appl. Biol.* 128:127–158.
- Sprague, G.F., and L.A. Tatum. 1942. General vs. specific combining ability in single crosses of corn. *J. Am. Soc. Agron.* 34:923–32.
- Trimble, M.W., and W.R. Fehr. 1983. Mixtures of soybean cultivars to minimize yield loss caused by deficiency chlorosis. *Crop Sci.* 23:691–694.
- USDA-National Agricultural Statistics Service. 1998. Iowa agricultural statistics. [Online]. [1 p.] Available at <http://www.nass.usda.gov/ia/> [cited June 2000; modified 20 April 2001; verified 22 May 2001]. USDA-NASS, Washington, DC.
- Weir, B.S. 1996. *Genetic Data Analysis II*. Sinauer Associates, Inc., Sunderland, MA.